PATCH USE UNDER PREDATION HAZARD:

EFFECTS OF THE RED IMPORTED FIRE ANT ON DEER MICE

FORAGING BEHAVIOR

A Thesis

by

WENDEE NICOLE HOLTCAMP

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 1995

Major Subject: Wildlife and Fisheries Sciences

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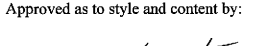

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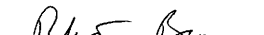

Robert Brown
(Head of Department)

May 1995

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Patch Use Under Predation Hazard:

Effect of the Red Imported Fire Ant on Deer Mice Foraging Behavior. (May 1995)

Wendee Nicole Holtcamp, B.S., Texas A&M University

Chair of Advisory Committee: Dr. William E. Grant

I compared patch use patterns of deer mice foraging in the presence and absence of a non-conventional predation hazard, red imported fire ants. Deer mice foraged for 60 min in an experimental arena containing two rich and two poor resource patches. All patches either had fire ants or did not have fire ants, and were filled with 5 or 16 whole sunflower seeds mixed in with 250 ml sand. Foraging strategy was identified by examining two aspects of patch use: density-dependence of resource harvest and over/underuse of rich patches relative to poor. Deer mice switched from a fixed search time strategy in the absence of fire ants to a Bayesian strategy in their presence. Resource harvest was density-independent in the absence of fire ants, meaning the mice harvested the same proportion of seeds from rich and poor patches. In the presence of fire ants, mice biased effort toward rich patches, resulting in positively density-dependent resource harvest. Mice also made significantly more patch visits, made more out-of-patch foraging bouts (taking seeds to protective cover), and spent more time foraging out of the resource patches in the presence of fire ants. Despite any

increased costs or lost time due to taking seeds to protective cover, mice harvested the same number of seeds in the same total time at the same overall harvest rate in the presence and absence of fire ants. The increased costs associated with foraging in the presence of fire ants were compensated for by biasing effort toward rich patches. Mice harvested more seeds, spent more time, and had a disproportionately higher harvest rate in rich patches in the presence of fire ants; there were no differences between use of rich and poor patches in their absence.

ACKNOWLEDGEMENTS

I would like to thank the members of my advisory committee, Dr. Bill Grant, Dr. Brad Vinson, and Dr. Kirk Winemiller for their help in the development of this research project. I am especially grateful to Dr. Grant, who helped me complete my research and graduate studies in record time. Sincere thanks to Dr. Mike Longnecker, who provided statistical advice on numerous occasions. Sherry Ellison maintained the fire ant colony, and provided various pieces of equipment. Thanks to Dr. Ira Greenbaum for providing me with the study animals, and to Dr. Vincent Cassone and the Animal Vivarium staff for providing a place to house the animals. I benefited greatly from discussions on my research with Joel Brown, Jon Chase, Amos Bouskila Ken Hotopp, and Peter Nonacs. Thanks to Dr. Ken Risenhoover for help in my early graduate career, to Christine Doucet for many helpful discussions of ecological concepts, and to Jason Price for helping with computer technology. My sincerest appreciation goes to Matthew and Savannah Holtcamp, who provided me with constant love and moral support throughout my graduate studies.

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INTRODUCTION

Optimal foraging theory

MacArthur and Pianka (1966) and Emlen (1966) simultaneously proposed the ideas that now form the heart of optimal foraging theory. Optimal foraging is based on the idea that, to the extent that foraging behavior may show heritable variation, natural selection should favor behavior or traits that maximize net reward for foraging effort. In optimal foraging models, the efficiency of foraging is measured in terms of some currency, usually energy but occasionally time (Schoener 1971).

Optimal foraging theory has stimulated a proliferation of research on foraging behavior (see Pyke et al. 1977, Krebs et al. 1983 for reviews), and optimal foraging models provide straightforward, testable predictions. Several authors have formalized these ideas into mathematical models that predict diet selection (Schoener 1969, 1971, Charnov 1973, Pulliam 1974, 1975, Werner and Hall 1974), optimal patch choice (Smith and Dawkins 1971, Charnov 1976), and optimal allocation of time to patches (Krebs et al. 1974, Charnov 1976, Charnov et al. 1976). Many studies have provided qualitative support for classic optimal foraging models (see Pyke et al. 1977), yet the specific quantitative predictions often have been less than accurate (Werner et al. 1983a, Dill 1987, Cassini et al. 1990, Newman 1991).

Ecology was the journal used as a model for style and format.

Foraging under predation hazard

A major drawback of classic optimality models is that they do not consider other attributes of fitness, such as survival. Obviously, an animal's future fitness will decrease dramatically if killed by a predator. In cases when maximizing energy intake and avoiding predation conflict, an animal might have to tradeoff foraging efficiency for survival (Sih 1980, Werner et al. 1983*b*, Lima 1985, Lima et al. 1985). Such tradeoffs imply foragers must actively make decisions which allow them to affect their own risk of predation. A growing body of evidence suggests that animals can indeed control their risk of predation through active decision-making (see Dill 1987, Lima and Dill 1989 for reviews). If a foraging animal must cope with these conflicting demands, observed behavior may not be in accordance with classic optimality predictions, which only consider energy maximization. Several recent models incorporate both energy and predator avoidance (Gilliam and Fraser 1987, Brown 1988, Abrahams and Dill 1989, Newman 1991, Brown 1992). These newly formulated models have received some empirical support (Gilliam and Fraser 1987, Gotceitas 1990, Brown et al. 1992), but we are still far from being able to predict an animal's behavior given a situation of conflicting demands. In this study, I examined patterns of patch use in the presence and absence of predation risk so that I could identify and evaluate the tradeoffs involved.

Patterns of patch use: foraging strategy

The marginal value theorem (MVT) was the earliest theoretical treatment of patch use and departure rules (Charnov 1973, 1976). The MVT gave quantitative predictions about when a forager should leave patches of varying quality, yet failed to tell us how the animal should decide when to leave a patch (Green 1984). Since then, several authors have hypothesized "stopping rules" that animals might use in deciding when to leave a given patch (Krebs et al. 1974, Charnov 1976, Oaten 1977, Green 1980, 1984, Iwasa et al. 1981, McNamara 1982, Stewart-Oaten 1982, McNair 1983). These stopping rules result in patterns of patch use that can be distinguished from one another (Valone and Brown 1989, Valone 1991). Which strategy a foraging animal should employ depends to a large extent on the amount of information the animal possesses about its environment.

The MVT assumed that an animal was omniscient, and hence had perfect knowledge of the environment (Charnov 1976). If a forager has complete knowledge of the environment, or if it can instantaneously and accurately assess patch quality upon encounter, the optimal decision is to leave each patch at the same quitting-harvest rate (Charnov 1976, Brown and Rosenzweig 1986, Brown 1988). The optimal quitting-harvest rate is that at which the costs of foraging in a patch (represented by missed opportunity costs, risk of predation, and metabolic costs) just equal the benefits derived from foraging in that patch (Brown 1988). On the opposite extreme, if an animal has no information about its foraging environment and is unable to acquire any

pre-harvest information, the optimal decision is to expend equal effort (amount of time) on all patches, in essence treating all patches identically (Stewart-Oaten 1982, McNair 1983). Most foragers probably have some amount of information that lies between the two extremes. Foraging under uncertainty (incomplete or imperfect information) has received much theoretical attention (Oaten 1977, Green 1980, McNamara and Houston 1980, Iwasa et al. 1981, McNair 1983, Clark and Mangel 1984), yet only recently have empirical investigations begun (Lima 1984, Valone and Brown 1989, Valone 1991).

There are five hypothesized foraging strategies that I will be investigating: prescient, Bayesian, fixed search time, fixed amount, and rate assessor. All of these strategies share certain common assumptions. First, all strategies assume that as resource density diminishes, the forager's harvest rate declines. This assumption allows one to directly translate quitting-resource densities into quitting-harvest rates, because if this assumption is met, quitting density represents a balancing of the forager's benefits and costs (Brown 1988). A quitting resource-density is simply the density of resources at the time the forager leaves a patch, and is known as giving up density (GUD). A second assumption of all but the fixed amount strategy, is that the forager is attempting to achieve a GUD in each patch. In other words, the animal is trying to equalize costs and benefits at a given patch, and hence will leave when benefits no longer exceed costs (if estimates of costs and benefits are unbiased). The ability of the forager to achieve its intended GUD reveals the extent of its patch assessment abilities (Valone and Brown 1989).

The five strategies I am investigating are distinguished by examining two aspects of a forager's patch use pattern: over- or underuse of *rich* patches relative to poor patches, and density-dependence of resource harvest (Valone and Brown 1989). Underuse of a patch means simply that the fitness of the animal would be enhanced by devoting more foraging time to that patch. Patch use, in this context, can be measured only relative to another patch. If patches are identical in all respects, we would expect an animal to leave both patches at the same GUD, and hence there should be no underuse of either patch. If two patches differ only in initial resource density, a forager may tend to over- or underuse the richer patch (Table 1). This is the first criterion we use to distinguish foraging strategy. The second criterion is the density-dependence of resource harvest. Resource harvest can be density-independent, or can be positively or negatively density-dependent. Positive density-dependence means that the probability of a resource item being harvested increases with patch resource density, and vice versa for negative density-dependence. Each of the five foraging strategies has a unique combination of the two criteria (Table 1). These strategies yield varying degrees of energy maximization, and have thus been categorized according to amount of information a forager has if it uses a particular strategy. In general, they assume that the more information an animal has the more it will maximize energy intake.

Prescient foraging

A prescient forager can accurately estimate the resource density of a patch before patch exploitation, through sensory capabilities or by remembering patch

TABLE 1. Predicted patterns and hypothetical results from each of the 5 foraging strategies being investigated. The table displays proportion of resources harvested, which allows us to determine density-dependence (eg. a greater proportion harvested from rich yields positive DD), and giving-up-density, which allows us to discern over- or underuse of rich patches relative to poor (if rich patch has a higher GUD, it is underused). Initial seed density of hypothetical rich and poor patches are 100g and 50g respectively.

			Rich patch		Poor patch	
Foraging strategy	Use of rich patch relative to poor	Density-dependence	GUD	Prop. harvested	GUD	Prop. harvested
Prescient	Same	Positive	20	0.8	20	0.6
Fixed time	Underused	Independent	40	0.6	20	0.6
Bayesian	Underused	Positive	40	0.6	25	0.5
Rate assessor	Overused	Positive	20	0.8	35	0.3
Fixed amount	Underused	Negative	55	0.45	5	0.9

qualities from prior exploitation (Valone 1991). Since the forager's estimate of patch resource density is unbiased, it will accurately assess resource density as the patch is depleted by its foraging, and will leave the patch when the remaining prey density equals its intended GUD. Hence, there should be no tendency to over- or underuse rich or poor patches. Because all patches are harvested to the same GUD, a greater proportion of resources will be taken from rich than poor patches, resulting in positively density-dependent resource harvest.

Bayesian foraging

A Bayesian forager uses knowledge of the distribution of patch types in the environment to estimate patch quality, but cannot instantaneously assess resource density of an encountered patch. Rather, it uses information gathered during exploitation of a given patch combined with its knowledge of the patch type distribution to estimate current patch quality. The accuracy of the forager's estimate of patch quality depends on whether a poor or rich patch is encountered (measured in relation to the environment's mean patch quality; Fig. 1). In poor patches, the estimate (E) is always above the actual patch resource density (A). As the forager depletes the patch, E approaches A, but the critical resource density (Q; intended GUD) is reached before E meets A. Thus, the actual resource density falls below Q and poor patches will be overutilized. In rich patches, the opposite occurs: E is always below A and this leads to underutilization. Although rich patches will have higher GUDs than poor patches, a greater proportion of resources will be harvested from rich patches, resulting

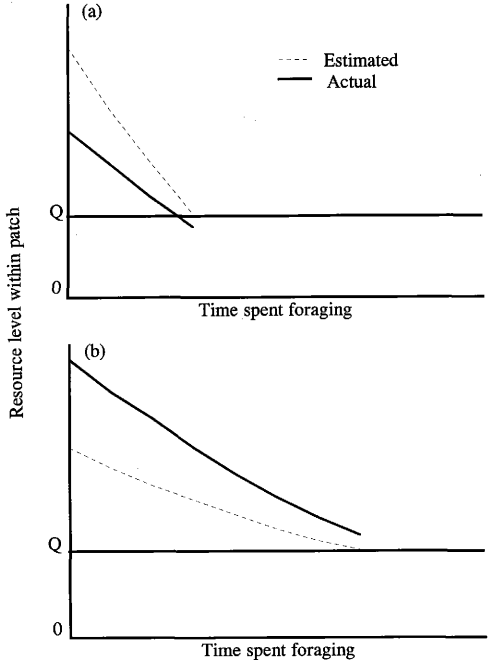

FIG. 1. Representation of how actual and estimated patch resource levels decline with time, according to Bayesian foraging, in (a) poor and (b) rich patches. Q represents the critical resource density at which foraging benefits balance costs. Poor patches are overused because the forager continues harvest beyond Q, and rich patches are underused because the forager leaves before the critical resource density is reached. Redrawn with permission from Valone and Brown (1989; Appendix C).

in positive density-dependence.

Rate assessor strategy

A forager using a rate assessor strategy has no pre-harvest information and uses only information on energy-intake rate obtained from current patch sampling (Valone and Brown 1989). The forager estimates harvest rate over the time it has spent in the patch, and leaves when its estimate drops to some critical level, its intended GUD. To equalize quitting-harvest rates, more time must be spent in rich patches than in poor patches, leading to overutilization of rich patches. This strategy yields positively density-dependent resource harvest.

Fixed amount strategy

A forager using a fixed amount strategy harvests the same amount from each encountered patch, regardless of initial patch quality. A fixed amount strategy will result in a higher proportion of food being harvested from poor than rich patches. In other words, resource harvest will be negatively density-dependent. In addition, rich patches will be underused.

Fixed search time strategy

A fixed time strategy results when a forager spends an equal amount of search time in each encountered patch, regardless of patch quality. Hence, resource harvest is density-independent and the forager will harvest the same proportion of resources from rich and poor patches. Thus, rich patches tend to have higher GUDs, meaning rich patches tend to be underutilized. An animal will maximize its average rate of resource

patches tend to be underutilized. An animal will maximize its average rate of resource harvest using this strategy when it can acquire no pre-harvest information on patch quality. The "fixed time" includes only search time, and not time spent handling resource items.

OBJECTIVES

In this study, I compared the foraging ecology and behavior of deer mice (Peromyscus maniculatus) in the presence versus the absence of the predation risk of red imported fire ants (Solenopsis invicta). My objectives were threefold:

(1) *Objective*: Compare harvest rate, attack rate, and handling time, parameters of Holling's disc equation (Holling 1959), in the presence versus the absence of fire ants. Attack rate is a proportionality constant that determines the encounter rate of a foraging animal with resources, and is determined by the species searching ability. Handling time is the time spent preparing a food item for consumption after it has been discovered (e.g., husking a seed). Additionally, I tested the assumption of diminishing returns on harvest rate, both in the presence and in the absence of fire ants, by fitting Holling's disc equation to a gain curve of seeds harvested versus foraging time.

Prediction: I predict that deer mice will experience diminishing returns in both the presence and absence of fire ants. I predict that handling time will be the same and harvest rate and attack rate will be lower in the presence than in the absence of fire ants.

(2) *Objective*: Compare observed patterns of patch use (over- or underuse of rich patches relative to poor patches, and density-dependence of resource harvest) both in the presence and the absence of fire ants to patterns predicted by each of five previously hypothesized foraging strategies: prescient, Bayesian, rate

assessor, fixed time, and fixed amount (Brown and Mitchell 1989, Valone and Brown 1989).

Prediction: I predict that patch use patterns of deer mice will match those predicted by the prescient strategy in the absence of fire ants, and will match those predicted by the Bayesian strategy in the presence of fire ants.

(3) *Objective*: Identify the tradeoffs made by deer mice foraging under predation risk by comparing several components of foraging behavior in the presence versus the absence of fire ants: number of patch visits, patch residence time, in-patch foraging time, proportion of seeds harvested, number of seeds harvested, final seed count (equivalent to GUD), time spent foraging in-patch per visit, number of seeds harvested per visit, seeds harvested per unit in-patch foraging time (in-patch harvest rate), out-of-patch foraging time, number of out-of-patch foraging bouts, amount of time spent on each out-of-patch foraging bout, total foraging time, and seeds harvested per unit foraging time (harvest rate).

Prediction: In the presence of fire ants, I predict that deer mouse patch residence time, in-patch foraging time, number of seeds harvested, time spent foraging in-patch per visit, seeds harvested per visit and harvest rate will be lower, and that number of patch visits, GUD, out-of-patch foraging time, number of out-of-patch foraging bouts, amount of time spent on each out-of-patch foraging bout, and total foraging time will be higher than in the absence of fire ants. I predict there will be no significant difference in proportion of seeds harvested and in-

patch harvest rate between fire ant present and absent trials.

This study is unique among foraging under predation hazard studies in that fire ants provide a non-conventional predation risk. Not only are fire ants exotic, but the risk of death upon encounter for a native rodent may be quite low, at least for healthy individuals who can escape from attacking ants. Although fire ants will consume a live-trapped small mammal within hours (Masser and Grant 1986, personal observation), the extent of fire ant-caused mortality of free-ranging rodents is unknown. Despite the possibility of fire ant-induced mortality being low, the threat of predation may actually be quite high. Imported fire ants prefer proteinaceous foods at most times of the year, are extremely efficient in locating food (Urbani and Kannowski 1974), are extremely abundant in the areas where they have established themselves (Porter et al. 1991), and have been known to prey on a wide variety of mammals and birds (Johnson 1961, Hill 1969, Mount et al. 1981, Ridlehuber 1982, Sikes and Arnold 1986, Flickinger 1989). Since the probability of a healthy small mammal remaining stationary while being consumed alive is low, the probability of fire ants altering a small mammal's patch use patterns is high. Deviations from "normal" patterns of patch use surely should impose some cost on a foraging small mammal. This study identified the tradeoffs deer mice made by deer mice foraging in the presence of red imported fire ants. The study also showed how fire ant predation hazard affected allocation of foraging effort between patches of varying quality. A justification for the choice of the study animals is provided in Appendix A.

METHODS

Animal husbandry

I obtained the 28 deer mice used in this study from a captive population maintained by Dr. Ira Greenbaum (Biology Dept., TAMU). All mice were siblings, and were first-generation captive-born. The animals were housed at the Animal Vivarium on the Texas A&M University campus in the Biological Sciences Building West. All animals were previously toe-clipped in a uniquely numbered sequence for identification.

Animals were provided with ad libitum food and water at all times, excluding the 24 hours prior to an experimental trial. Diet consisted of 4% fat laboratory rodent chow (Harlan Teklad, Madison, WI) and unhusked striped sunflower seeds. Animals were housed in plastic bins in groups of 4-6, with males and females separated. Bins were kept 1/3 full with Beta-Chip sanitary wood chips (Northeastern Products Corp., Memphis, TN) and were equipped with one small tin coffee can for shelter, a stainless steel feed dish (Research Equipment Co., Bryan, TX), and a 15.24 x 15.24 x 6.35 cm plastic Rubbermaid® square (Rubbermaid® Inc., Wooster, OH) filled with sand and sunflower seeds. Cotton squares (Ancare Corp., Bellmore, NY) were provided for bedding material. Mice were fed daily, and bins were cleaned weekly. The mice were kept on a schedule of light from 0900-1900.

Experimental design

The experiment consisted of foraging trials conducted within an 81.28 x 91.44 x

30.48 cm (length x width x height) clear plexiglass box (experimental arena), which had a clear plexiglass lid. Water was available to the mouse within the arena via a water bottle inverted through the arena lid. Four open-topped plastic Rubbermaid® square boxes (15.24 x 15.24 x 6.35 cm) simulated habitat patches within the arena (Fig. 2). The "patch" boxes were filled with a pre-measured number of unhusked sunflower seeds mixed in with 250 ml of sand. Two of these patches were rich patches (15 seeds) and two were poor patches (6 seeds). Poor and rich were defined relative to the environment's mean patch quality.

Seed densities of poor and rich patches were chosen based on pre-experimental satiation trials. In the satiation trials, I determined the amount deer mice would eat within a 12-hour period (overnight). I then ensured that the number of seeds divided among the two rich and two poor patches was high enough so that the mice would not deplete all patches to a GUD of zero, but low enough to ensure diminishing returns on resource harvest.

Before any experimentation began, all mice were acclimated to fire ants and the experimental arena in a 60 min exposure trial. In each exposure trial, all mice housed within the same bin (4-6) were placed in the arena and allowed to explore for 60 min. The arena contained 6 open-topped plastic Rubbermaid® square boxes (15.24 x 15.24 x 6.35 cm), each filled with 5 g millet mixed in with 250 ml sand, and 50 fire ants.

The experimental design consisted of 24 paired replications of the two treatments (fire ant present and absent), with each mouse used once in a fire ant present

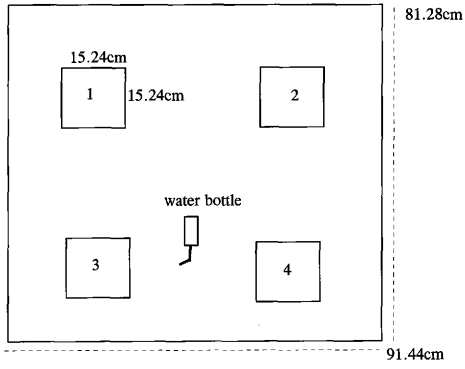

FIG. 2. Diagrammatic representation of experimental arena.

and once in a fire ant absent trial (Fig 3). Each replication consisted of a 3-trial sequence: two trials without fire ants (the first to enable the mouse to learn patch quality and distribution), and one trial with fire ants present. Data from trial one (learning trial) were not considered in this study. The location of rich and poor patches within the arena was randomized for each mouse, but remained the same for a given mouse's 3-trial sequence. The order of mice participating in the trials was selected as follows. One of the five bins was selected at random, and all mice from that bin were used in the 3-trial sequence before moving on to the next bin. The first mouse captured from the selected bin was food-deprived in a solitary bin for 8-12 h prior to the learning trial. After trial one and two, the mouse was returned to its solitary bin and food-deprived, for 8-12 h, until the next trial. After the 3-trial sequence, the mouse was placed in a third bin, apart from the other mice that had not yet been used in the experiment.

In trials with fire ants present, 100 fire ants were placed within the patch boxes in addition to the sunflower seeds and sand. To prevent fire ants from escaping the patch boxes, fluon® AD-1 (polytetrafluoroethylene resin; Imperial Chemical Industries, Wilmington, DE) was painted around the entire inside edge of each patch box (Imperial Chemical Industries 1985). As this substance dries, it creates a substance too "slippery" for fire ants to crawl up. Statistical analyses were performed to ensure differences in deer mouse behavior were not due to fluon presence in trial 3 (Appendix C). None were significant. A polygyne fire ant colony was maintained at the

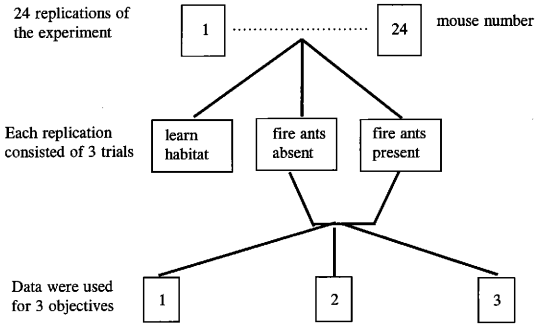

FIG. 3. Flow chart of experimental design. Details are contained within the text.

Entomology Research Laboratory (ERL) on the Texas A&M University campus. Ants were kept on a diet of approximately 50% mealworm and 50% ant diet (S. Ellison, pers. comm.).

During each trial, I recorded time of entry into and exit from each patch on a palmtop computer. Any time spent foraging outside of a patch also was recorded. Out-of-patch-foraging was associated solely with a mouse consuming a seed taken from a patch. Trials were conducted between the hours of 0500-0900 and 1900-2100, which were hours of darkness for the rodents. All foraging trials were videotaped with an overhead camcorder. Since I videotaped the trials, and also because I was present recording data, three 25-Watt red light bulbs (GE® Party Bulb, Cleveland, OH) were used for illumination. After each trial, I sifted the sand/seed mixture from each patch through a sieve to recover and count uneaten seeds. All statistical analyses were performed using Statistical Analysis Software Version 6 (SAS® Institute Inc., 1993). To avoid the problem of pseudoreplication brought about by my use of two rich and two poor patches, I obtained rich patch and poor patch totals for all data values, and used the totals as the input data for all statistical analyses. Thus, for each trial, one line of data was associated with rich patches, and one with poor patches.

Objective 1 - Holling's disc equation

Harvest rate, attack rate, and handling time were compared between mice foraging in the presence versus the absence of fire ants. I used a modified version of Holling's disc equation (Holling 1959):

$$t = (1/a)\ ln(N_0/N_f) + h\ (N_0 - N_f) \quad (1)$$

in statistical analyses. In the above equation, t is foraging time, a is attack rate, h is handling time, N_0 is initial seed density, and N_f is final seed density.

I used multiple linear regression to determine if mice were experiencing diminishing returns in their harvest rate, according to methods outlined in Kotler and Brown (1990). In the regression analysis, t was the dependent variable and $ln(N_0/N_f)$ and $(N_0 - N_f)$ were independent variables. Foraging time (t) was calculated according to the following equation,

$$t = I + (O/F_t \cdot F_p) \quad (2)$$

where I is in-patch foraging time, O is out-of-patch foraging time, F_t is total number of patch visits, and F_p is number of visits to that patch type (rich or poor). This equation allowed me to divide out-of-patch foraging time in a way that was scaled to the number of visits made to each patch type. This scaling equation was necessary since initial and final seed densities were grouped by patch type, but total foraging time (in-patch plus out-of-patch) was not. All R^2 values were adjusted for number of terms in the model.

If this form of Holling's disc equation (Eq. 1) fits the data ($P < .05$), then we can assume that mice experienced diminishing returns in their rate of seed harvest as they depleted a patch. The output of the regression analysis also provides estimates of handling time (h) and attack rate (a), which are simply the coefficient of $(N_0 - N_f)$ and the reciprocal of the coefficient of $ln\ (N_0/N_f)$, respectively. One regression was run for fire ant present trials and one for fire ant absent trials.

I used a blocked two-factor analysis of covariance (ANCOVA) to compare harvest rate in the presence versus the absence of fire ants (Kotler and Brown 1990). Foraging time (t), calculated as above, was the dependent variable, $ln(N_0/N_f)$ and $(N_0 - N_f)$ were two covariates, treatment (fire ants present/absent) and patch quality (rich/poor) were group variables, and individual was the blocking factor. If the above ANCOVA shows that harvest rate is significantly different for mice foraging in the presence of fire ants, then we can test whether attack rate or handling time (components of harvest rate), or both, are responsible for the difference. The same blocked two-factor ANCOVA is used, except that here we add additional terms for interaction between fire ant treatment and each covariate. If significant interaction exists ($P < .05$), this indicates a significant effect of fire ant treatment on attack rate or handling time. One outlying data point was excluded from the aforementioned analyses. Based on personal observation, I believe the foraging time recorded (2506 s) was overestimated, as the mouse likely was engaging in non-foraging activity within the patch.

Objective 2 - foraging strategy

Patch use patterns observed by deer mice foraging in the presence and absence of fire ants were compared to patterns predicted by five foraging strategies (Table 1). I predicted that deer mice would switch from a prescient to a Bayesian strategy when exposed to fire ants. Two patch-use patterns were examined in order to differentiate among the five strategies: over- or underuse of rich patches relative to poor, and density-dependence of resource harvest (Valone and Brown 1989). For both of these

criteria, blocked one-factor ANOVAs were used, where GUD or proportion harvested was the dependent variable, patch quality was the independent variable, and individual was the blocking factor (Ott 1993). I performed separate ANOVAs for fire ant absent and present data. I used an arcsin transformation for the proportion harvested ANOVA, taking the square-root of the arcsin of proportion harvested (Ott 1993). Foraging strategy then was determined by matching observed patch use patterns with those predicted by each of the five foraging strategies (Table 1).

In order to consider giving up densities equivalent to quitting harvest-rates, I must assume the foraging deer mice experience diminishing returns on their harvest rate as seed density is depleted. This assumption is implicit in Holling's disc equation (Holling 1959), and hence if the gain curves obtained from objective 1 fit reasonably well to this equation ($P < .05$), this assumption is valid.

Objective 3 - foraging behavior

I compared several aspects of foraging behavior between mice foraging in the presence versus the absence of fire ants: number of patch visits, patch residence time, in-patch foraging time, proportion of seeds harvested, number of seeds harvested, final seed count (equivalent to GUD), time spent foraging in-patch per visit, number of seeds harvested per visit, seeds harvested per unit in-patch foraging time (in-patch harvest rate), out-of-patch foraging time, number of out-of-patch foraging bouts, amount of time spent on each out-of-patch foraging bout, total foraging time, and number of seeds eaten per second (harvest rate). Patch residence time is total time spent within a patch,

including both foraging and non-foraging time. Time foraging in-patch per visit was calculated by divided in-patch foraging time by number of patch visits. Number of seeds eaten per visit was calculated by dividing total seeds harvested by number of patch visits. Amount of time foraging out-of-patch per patch visit was obtained by dividing total out-of-patch foraging time by the number of out-of-patch foraging bouts. Total foraging time is the sum of in-patch and out-of-patch foraging.

Blocked two-factor ANOVAs were used to compare number of patch visits, patch residence time, in-patch foraging time, proportion of seeds harvested, number of seeds harvested, final seed count (GUD), time spent foraging in-patch per visit, number of seeds harvested per visit, and seeds harvested per unit in-patch foraging time (in-patch harvest rate). For these analyses, fire ants (presence/ absence) and patch quality (rich/ poor) were the independent variables, and individual was the blocking factor (Ott 1993). In addition, I performed Tukey's multiple comparison tests (Ott 1993) to determine if means were different for the four treatments. I used natural log transformations for all dependent variables, except GUD, proportion of seeds harvested, and in-patch harvest rate, to improve the normality of the residuals (Ott 1993). I used an arcsin transformation for the proportion harvested data, taking the square-root of the arcsin of proportion harvested (Ott 1993). All values presented in results are backtransformations of the means.

Blocked one-factor ANOVAs were used to compare out-of-patch foraging time, number of out-of-patch foraging bouts, amount of time spent on each out-of-patch

patch foraging bout, total foraging time, and seeds harvested per unit foraging time (harvest rate) between fire ant present and absent trials. Individual was the blocking factor. Patch quality could not be used as a second factor in these analyses because out-of-patch foraging data was not associated with any particular patch (rich/ poor). Hence, any calculation that included out-of-patch foraging had to be analyzed with rich and poor patch data combined. The same outlying data point excluded in the analyses for objective 1 also was excluded in these analyses.

RESULTS

Objective 1 - Holling's disc equation

The multiple regression that fit Holling's disc equation to the data showed that deer mice experienced diminishing returns on their rate of resource harvest in both the presence ($F = 64.2$, $P < .0001$, $R^2 = 0.7290$) and absence ($F = 32.9$, $P < .0001$, $R^2 = 0.5814$) of fire ants. Handling time estimates are 634.6 $s \cdot g^{-1}$ in the presence of fire ants ($t = 5.0$, $P < .0001$) and 717.8 $s \cdot g^{-1}$ in the absence of fire ants ($t = 6.2$, $P < .0001$). Reliable estimates for attack rate could not be made because the parameter estimates were not significantly different from zero in both the presence and absence of fire ants ($P > .05$). This indicates foraging was dominated by handling time, and not search time, in both the presence and absence of fire ants.

ANCOVA results implied harvest rates did not significantly differ between deer mice foraging in the presence or absence of fire ants ($F = 0.6$, $P = .44$). The ANCOVA that tested for interaction between each covariate and fire ant presence showed that attack rates ($F = 1.49$, $P = .23$) and handling times ($F = 1.12$, $P = .29$) were not affected by fire ants. Although not significant, handling time was lower in the presence of fire ants (see above).

Since harvest rates were not significantly different for deer mice foraging in the presence versus the absence of fire ants, data were pooled and the regression was performed on the pooled data. As expected, the resulting regression also showed that deer mice experienced diminishing returns ($F = 101.4$, $P < .0001$, $R^2 = 0.6880$).

Objective 2 - foraging strategy

In both fire ant present and absent trials, GUDs of rich patches were significantly higher than GUDs of poor patches ($F = 64.95$, $P < .0001$; $F = 140.32$, $P < .0001$ respectively), indicating mice underused rich patches in both cases. In fire ant absent trials, there was no significant difference in proportion of seeds harvested between rich and poor patches ($F = 1.1$, $P = .31$), indicating density-independent resource harvest. In fire ant present trials, mice harvested a significantly higher proportion of seeds from rich patches ($F = 14.29$, $P < .001$), indicating positively density-dependent resource harvest. Referring to Table 1, the results indicate deer mice used a fixed search time foraging strategy when fire ants were absent, and a Bayesian strategy when fire ants were present.

Objective 3 - foraging behavior

Table 2 displays results from all two-factor ANOVAs. As predicted, number of patch visits (Fig. 4) was significantly higher when fire ants were present (see Table 2 for specific P-values; all significant relationships have a $P < .05$). In addition, mice made significantly more visits to rich patches than to poor patches (Fig. 4). There was significant interaction between fire ant presence and patch quality for this variable. The interaction indicated that when fire ants were absent there was no difference in number of visits made to rich and poor patches, but when fire ants were present mice made significantly more visits to rich patches than to poor patches (Fig. 4).

Contrary to my prediction, neither patch residence time (Fig. 5) nor in-patch

TABLE 2. Results of all two-factor ANOVAs comparing attributes of deer mice foraging behavior in the presence versus the absence of fire ants, and between patches of poor versus rich quality. Degrees of freedom are 26,68 for the model and 1,68 for individual effects, except where otherwise noted.

	Model	Fire Ants	Patch Quality	Interaction
Variable	F	F	F	F
Number of patch visits	2.99^{***}	$16.72^{\dagger}$	3.02	4.03^{*}
Patch residence time	2.51^{**}	2.04	10.75^{**}	1.18
In-patch foraging time	$3.36^{\dagger}$	1.74	$17.91^{\dagger}$	0.74
Proportion of seeds harvested[A]	2.36^{**}	0.07	3.17	11.28^{**}
Seeds harvested[A]	$10.23^{\dagger}$	2.15	$206.85^{\dagger}$	10.96^{**}
Giving up density (final seed count)[A]	$10.23^{\dagger}$	2.15	$206.85^{\dagger}$	10.96^{**}
Time foraging in-patch per visit[B]	$3.57^{\dagger}$	$40.57^{\dagger}$	4.95^{*}	0.01
Seeds harvested per visit	2.81^{***}	12.32^{***}	14.49^{***}	5.36^{*}
In-patch harvest rate	$3.03^{\dagger}$	5.33^{*}	11.45^{**}	5.36^{*}

[A] df=26,69 (model), 1,68 (individual); [B] df=26,67 (model), 1,67 (individual).
* $P < .05$; ** $P < .01$; *** $P < .001$; † $P < .0001$.

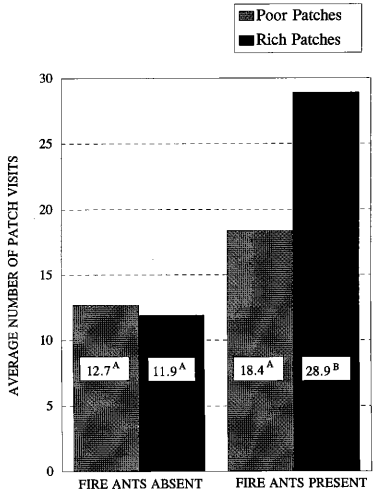

FIG. 4. Comparison of average number of patch visits made to rich and poor patches by deer mice foraging in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

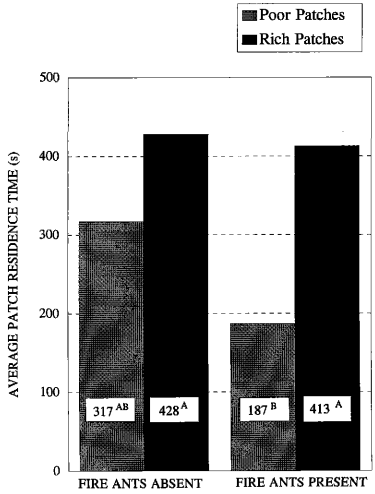

FIG. 5. Comparison of average patch residence time in rich and poor patches in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

foraging time (Fig. 6) were affected directly by fire ants. Although the interaction term was not a significant contributor to the model for either variable (Table 2), Tukey's W showed that there was interaction between patch quality and fire ant presence for both in-patch foraging time (Fig. 6) and patch residence time (Fig. 5). As with number of patch visits (presented above), when fire ants were absent there was no significant difference in patch residence time or in-patch foraging time between rich and poor patches. However, when fire ants were present, mice had significantly higher patch residence (Fig. 5) and in-patch foraging times (Fig. 6) in rich patches than in poor patches. Results also showed that patch quality significantly affected patch residence time and in-patch foraging time; mice spent significantly more time in rich than in poor patches (Table 2).

Proportion of seeds harvested also showed significant interaction, but no direct effects of fire ant presence or patch quality (Fig. 7). When fire ants were absent, there was no difference in proportion of seeds harvested from rich or poor patches, but when fire ants were present, mice harvested a significantly higher proportion of seeds from rich patches (Fig. 7).

Neither seeds harvested (Fig. 8) nor GUD (Fig. 9) was affected directly by fire ant presence. However, results indicated significant interaction between fire ant presence and patch quality for both of these variables (Table 2). Deer mice harvested the same number of seeds from poor patches regardless of fire ant presence or absence, but harvested significantly more seeds from rich patches when fire ants were present

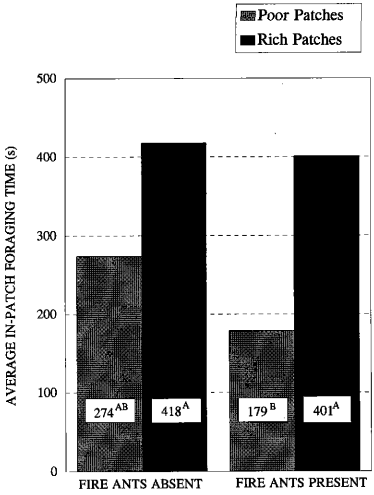

FIG. 6. Comparison of average in-patch foraging time in rich and poor patches in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

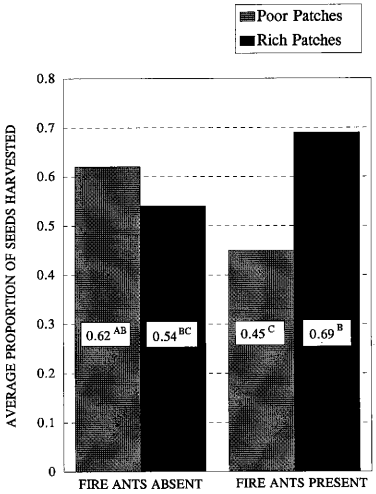

FIG. 7. Comparison of average proportion of seeds harvested from rich and poor patches in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

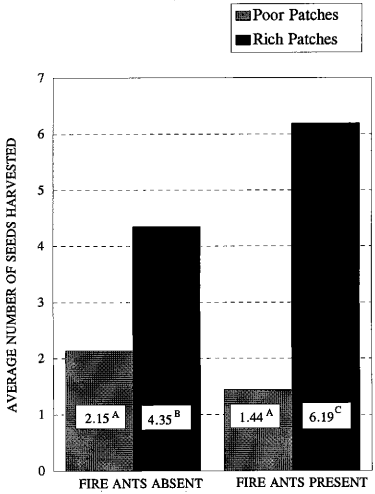

FIG. 8. Comparison of average number of seeds harvested from rich and poor patches in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

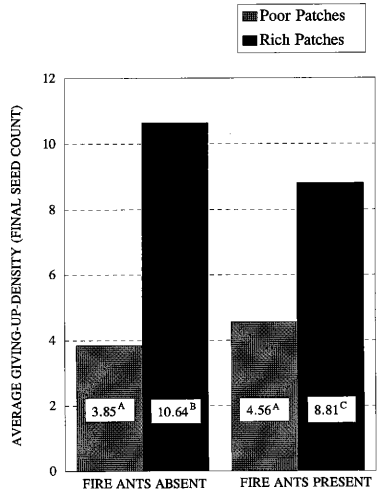

FIG. 9. Comparison of average number of seeds remaining in rich and poor patches in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

than when absent (Fig. 8). Likewise, deer mice left poor patches at the same GUD regardless of fire ant presence or absence, but left rich patches at a significantly lower GUD when fire ants were present (Fig. 9). Statistical results are identical for seeds harvested and GUD because one is simply the reciprocal of the other. However, both are presented because they are helpful in interpreting results, and they provide different information about the system.

Time spent foraging in-patch per visit (Fig. 10), and average number of seeds harvested per visit (Fig. 11) were significantly lower when fire ants were present, as predicted. Although I made no a priori predictions regarding patch quality, it is interesting to note that deer mice spent significantly more time foraging in-patch per visit (Fig. 10), and harvested significantly more seeds per visit (Fig. 11) in rich patches than in poor patches. There was no significant interaction between fire ants and patch quality for time foraging in-patch per visit (Fig. 10, Table 2). For average number of seeds harvested per visit, the interaction indicated that when fire ants were absent mice harvested more seeds per visit from rich patches than from poor. However, when fire ants were present there was no difference in seeds harvested per visit between rich and poor patches (Fig. 11).

In-patch harvest rate was significantly affected by fire ants, patch quality, and the interaction of these terms (Fig. 12). In-patch harvest rate was always higher in rich patches, as expected. In addition, it was disproportionately higher in rich patches when fire ants were present (Fig. 12).

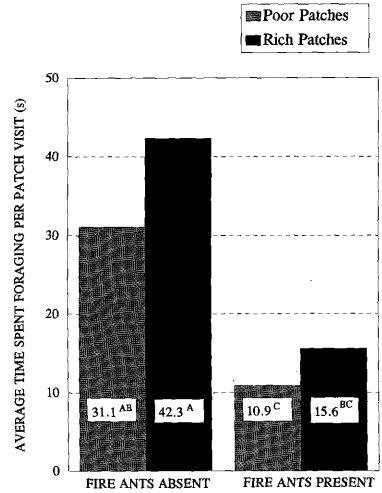

FIG. 10. Comparison of average time spent foraging in rich and poor patches per patch visit by deer mice foraging in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

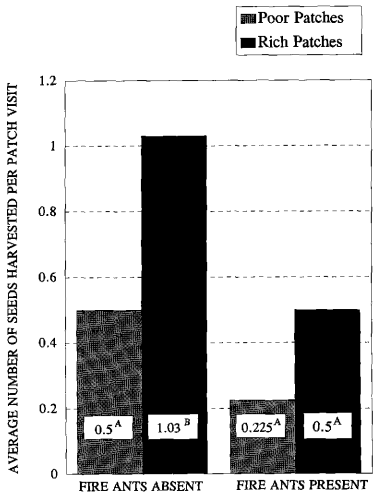

FIG. 11. Comparison of average number of seeds harvested from rich and poor patches per patch visit by deer mice foraging in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

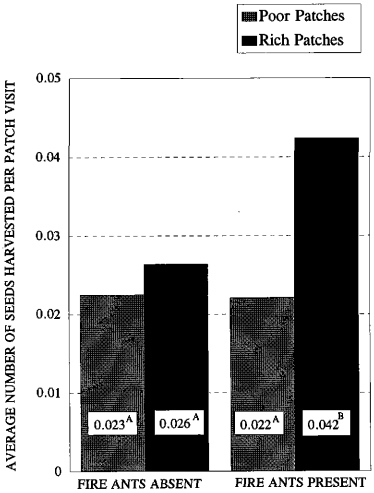

FIG. 12. Comparison of average in-patch harvest rate (number of seeds harvested per unit in-patch foraging time) in rich and poor patches by deer mice foraging in the presence versus the absence of fire ants. Numbers accompanied by the same letter are not significantly different ($P > .05$).

Table 3 presents results from all one-factor ANOVAs. As predicted, out-of-patch foraging time (Fig. 13), number of out-of-patch foraging bouts (Fig. 14), and amount of time spent on each out-of-patch foraging bout (Fig. 15) were significantly higher when fire ants were present. Contrary to my predictions, there was no difference in total foraging time (Fig. 16) or seeds harvested per unit foraging time (overall harvest rate; Fig. 17) between fire ant present and absent trials. Although not significant, total foraging time was higher when fire ants were present than absent, as predicted (Fig. 16). Overall harvest rate (seeds harvested per unit total foraging time) was almost identical in the presence and absence of fire ants (Fig. 17).

TABLE 3. Results of all one-factor ANOVAs comparing attributes of deer mice foraging behavior in the presence versus the absence of fire ants. Degrees of freedom are 24,23 for the model and 1,23 for fire ants unless otherwise noted.

	Model	Fire Ants
Variable	F	F
Out-of-patch foraging time (s)	3.82^{***}	$22.05^{\dagger}$
Number of out-of-patch foraging bouts	3.39^{**}	$30.45^{\dagger}$
Amount of time spent on each out-of-patch foraging bout (s)[A]	1.08	8.73^{**}
Total foraging time (s)	4.01^{***}	1.23
Harvest rate (seeds harvested per unit total foraging time)	2.88^{**}	2.99

[A] df=24,19.

** $P < .01$; *** $P < .001$; † $P < .0001$.

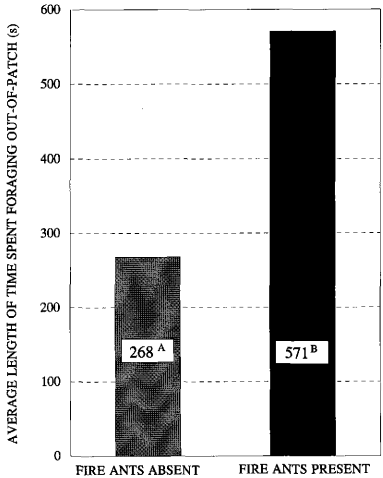

FIG. 13. Comparison of the average length of time spent foraging out-of-patch between deer mice foraging in the presence versus the absence of fire ants. Out-of-patch foraging is associated with the mouse taking a seed to protective cover (away from fire ant predation risk). Numbers accompanied by the same letter are not significantly different ($P > .05$).

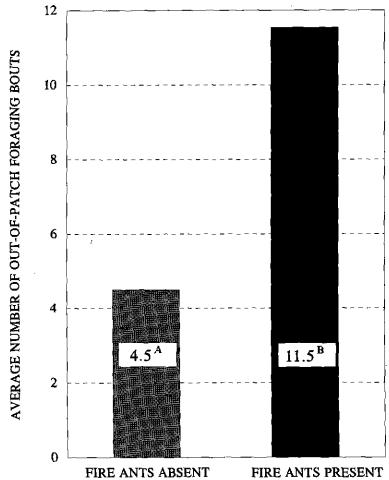

FIG. 14. Comparison of the average number of out-of-patch foraging bouts between deer mice foraging in the presence versus the absence of fire ants. An out-of-patch foraging bout is associated with the mouse taking a seed to protective cover (away from fire ant predation risk). Numbers accompanied by the same letter are not significantly different ($P > .05$).

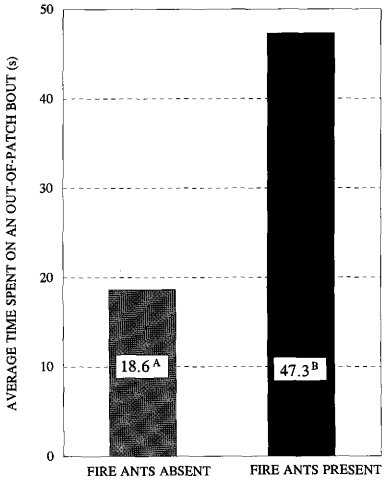

FIG. 15. Comparison of the average length of time spent on an out-of-patch foraging bout by deer mice foraging in the presence versus the absence of fire ants. An out-of-patch foraging bout is associated with the mouse taking a seed to protective cover (away from fire ant predation risk). Numbers accompanied by the same letter are not significantly different ($P > .05$).

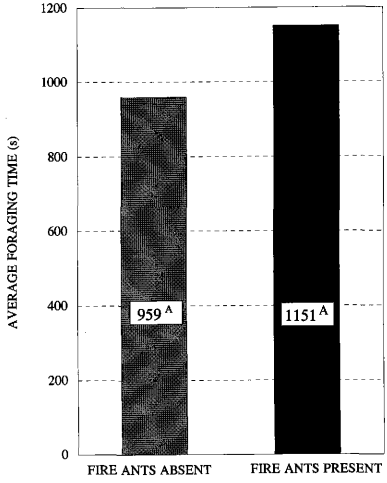

FIG. 16. Comparison of the average foraging time between deer mice foraging in the presence versus the absence of fire ants. Foraging time includes both time spent foraging in-patch and out-of-patch. Numbers accompanied by the same letter are not significantly different ($P > .05$).

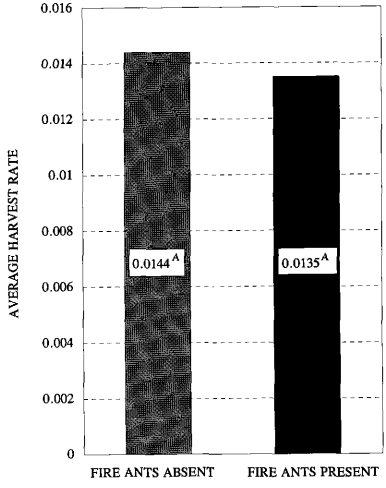

FIG. 17. Comparison of the average harvest rate between deer mice foraging in the presence versus the absence of fire ants. Harvest rate is calculated as number of seeds eaten divided by total foraging time. Numbers accompanied by the same letter are not significantly different ($P > .05$).

DISCUSSION

My results show substantial differences in the foraging ecology and behavior of deer mice in the presence versus the absence of fire ants. When foraging under the predation risk of imported fire ants, deer mice switched from a less energetically efficient strategy (fixed search time) to a more efficient one (Bayesian), and biased foraging effort toward rich patches. Deer mice also showed a significant increase in number of patch visits and number of out-of-patch foraging bouts (which was associated with taking a seed to cover). Taking seeds to cover must incur an increased energetic cost since the animal has to expend extra energy to carry the seed to cover, and spend time that it could be devoting to foraging or alternative activities (Lima and Valone 1986). Despite any increased costs associated with foraging under the threat of predation, deer mice showed no differences in total seeds harvested, total foraging time, or overall harvest rate. I will discuss several lines of evidence that suggest deer mice were able to become more efficient foragers in the presence of fire ants.

Deer mice foraging in the presence of fire ants made significantly more out-of-patch foraging bouts, spent more time foraging out-of-patch, and spent significantly longer on each out-of-patch foraging bout (Table 3). Despite the difference in out-of-patch foraging, there was no significant difference in total foraging time. Figure 18 displays total foraging time divided between in-patch and out-of-patch foraging for fire ant present and absent trials. Total number of seeds harvested and overall harvest rate also were not significantly different between fire ant present and absent trials. If deer

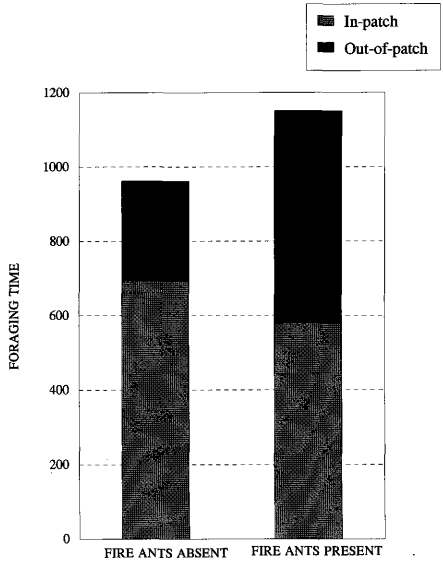

FIG. 18. Comparison of total foraging time for deer mice in the presence and absence of fire ants, broken down into in-patch and out-of-patch foraging time.

mice harvested the same number of seeds in the same total foraging time at the same overall harvest rate, yet spent significantly more time foraging out-of-patch and made significantly more patch visits, how did they make up this extra time? Somehow the mice had to become more efficient foragers when in the presence of fire ants. The answer can be revealed by examining the use of rich patches relative to poor patches.

When foraging in the presence of fire ants, deer mice biased effort toward rich patches, whereas there was no such trend in the absence of fire ants. Deer mice made significantly more patch visits, had higher patch residence times and in-patch foraging times, and harvested a higher proportion of seeds from rich than poor patches when in the presence of fire ants; there were no significant differences in these four variables in deer mice foraging in the absence of fire ants. If the mice were able to make up for increased costs or lost time due to taking seeds to cover, they must have increased their within-patch harvest rate in the presence of fire ants. Indeed, in-patch harvest rate was was significantly higher in the presence of fire ants (Table 2). The preference for rich patches and increased in-patch harvest rate in the presence of fire ants strongly suggests that deer mice were able to forage more efficiently when under the threat of predation.

When fire ants were absent, deer mice used a fixed search time strategy. This strategy maximizes the average rate of energy intake when a forager has no pre-harvest information, and also cannot gain any information from patch sampling (Iwasa et al. 1981, Stewart-Oaten 1982, McNair 1983). When fire ants were present, mice switched to a Bayesian strategy. The Bayesian strategy yields a higher rate of energy intake than

the fixed search time strategy (Iwasa et al. 1981), and hence it appears mice became more efficient foragers in the presence of fire ants.

The foraging strategies I investigated have been associated with differing degrees of pre-harvest information (Valone and Brown 1989). It has been assumed that animals that have more information will tend to maximize energy intake to a greater extent. Thus it is possible that the switch in foraging strategy was at least partially due to a learning effect, since all mice participated in a fire ant absent trial before a fire ant present trial. However, foragers may not maximize energy intake for a variety of reasons, only one of them being lack of information. In addition, while it is certainly possible that the mice gained some information over the 3-trial sequence, it is unlikely the mice went from having no information (the circumstances under which the fixed search time strategy is optimal) in trial two of the sequence to having both knowledge of patch distribution, and patch sampling abilities (qualities necessary for Bayesian sampling) in trial three. I suggest that the mice had the knowledge in both the fire ant absent and present trials, but only chose to act upon this information when in the face of increased costs (predation risk).

I found that GUD'S were significantly lower in rich patches in the presence of fire ants. This result appears to contradict the predictions made by Brown's (1988) "H = C + P + MOC" rule. This rule states that a forager should leave each patch when the harvest rate (H) no longer exceeds the sum of metabolic (C), predation (P), and missed opportunity costs (MOC) of foraging, which is an extension of Charnov's (1976)

Marginal Value Theorem. The model predicts that a forager should demand higher feeding rates in the presence of increased predation risk. Brown (1988) claims that as long as the assumption of diminishing returns is met, GUDs directly correlate with quitting-harvest rates. Thus my results either contradict Brown's (1988) model, or GUDs are not providing an accurate surrogate for quitting-harvest rates. To distinguish between these possibilities, I examined in-patch harvest rates (Fig. 13), and found that they were significantly higher when fire ants were present. Thus the model's predictions are supported, but the use of GUDs as surrogates for quitting-harvest rates is strongly questioned.

The use of GUDs in place of quitting-harvest rates implicitly assumes that, for a given species, at a given seed density, harvest rate is a constant. Deer mice were able to harvest patches to a lower final seed density (GUD) but maintained a higher average in-patch harvest rate. This suggests the deer mice were able to alter their rate of harvest, perhaps by decreasing handling times. Handling times were almost 100 $s \cdot g^{-1}$ lower when fire ants were present (634.6 $s \cdot g^{-1}$ in the presence of fire ants versus 717.8 $s \cdot g^{-1}$ in their absence), although statistically these differences were not significant. If an animal is able to alter its harvest rate at will, if it is not already operating at the maximal possible harvest rate, then GUDs will not provide an accurate surrogate for quitting-harvest rate, as in my data.

Other studies have suggested that animals may become more efficient foragers when under threat of predation. Newman et al. (1988) found that handling times

decreased under the threat of predation. Grey squirrels (Sciurus carolinensis) ate the same quantity of seeds farther from cover (increased predation risk) but ate them significantly faster, due to decreased handling times. These results almost directly parallel my results, and are particularly noteworthy because handling times typically are considered constraints on a forager's efficiency, and are assumed to be constant for a given species. If a forager is not already operating at its maximal possible harvest rate, then a forager's efficiency is not necessarily constrained by its morphological adaptations.

Hay and Fuller (1981) found that the ratio of preferred to nonpreferred seeds harvested by heteromyid rodents changed from 2.5:1 under canopies (low predation risk) to 7.5:1 in the open (high predation risk). Bowers (1988) found similar results on seed preferences of heteromyids in bush compared to open sites, and full moon compared to new moon nights. Forkman (1991) provides an example of improved foraging efficiency with increased environmental variation. He found that Mongolian gerbils (Meriones unguiculatus) took fewer seeds from a less profitable patch when environmental variability was increased, hence becoming more like short-term energy maximizers. Although environmental variability provides a different type of "risk" than predation (Real and Caraco 1986), this study suggests it may result in the same types of behavioral tradeoffs made by foraging animals.

In order for foragers to become more efficient in risky situations, they must have been operating at some less-than-maximal efficiency when risk was lower. This

idea is contrary to current patch use theory, which assumes that, all else being equal, a forager will choose the most profitable patch (Stephens and Krebs 1986). In situations where a forager does not choose a diet, patch, or habitat that maximizes energy-intake, it is likely that the fitness value of information gathering may be more important than strict energy-maximization (Inglis and Ferguson 1986).

Future studies

While this study compared the behavior of deer mice in the presence and absence of fire ants, and elucidated some very interesting results, there was no opportunity for the mice to choose actively between fire ant present and absent patches in the same trial. Such a study would allow a quantification of the marginal rate of substitution of energy for predation risk (Gilliam and Fraser 1987, Abrahams and Dill 1989, Nonacs and Dill 1990) by determining precisely what level of food offsets the predation risk of fire ants. Hunger also plays a vital role in the interplay between predation risk and the importance of maximizing energy intake. Future studies of this system should link hunger level, predation risk, and food intake.

CONCLUSIONS

My results suggest that deer mice foraging in the presence of fire ants were able to become more efficient foragers by altering their patterns of patch use. Despite making significantly more patch visits and out-of-patch foraging bouts, deer mice under the predation risk of fire ants harvested the same number of seeds in the same total foraging time at the same overall harvest rate. This likely was due to the bias of foraging effort toward the more profitable rich patches and the increased in-patch harvest rate in the presence of fire ants. This bias of effort toward rich patches also is reflected in the switch from a fixed search time to a Bayesian foraging strategy.

My results support Brown's (1988) "H = C + P + MOC" rule, which is an extension of Charnov's (1976) Marginal Value Theorem that considers components of fitness other than energy maximization, although the use of GUDs in place of quitting-harvest rates is strongly questioned. A major challenge of the future will be to quantify the values that animals place on various activities associated with fitness so that we can predict what tradeoffs an animal will make in a given situation.

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APPENDIX A

ECOLOGY OF THE STUDY ANIMALS

Red imported fire ants came to the United States from South America's Pantanal floodplain in the 1930's via a ship bound for the port of Mobile, Alabama (Lofgren 1986). Presumably because of their origin in the frequently flooded Pantanal, red fire ants are well adapted to disturbance, and have been able to rapidly colonize habitat in the southeast US. Within the past 10-15 years, a new form of fire ants has been found which exists in multiple queen, or polygyne, colonies (Vinson and Sorensen 1986). Not only does the polygyne form have thousands more fire ants per colony, and 200-300 queens per colony, mound densities can be 10 times higher than in areas with single-queen (monogyne) colonies (Vinson and Sorensen 1986). The original single-queen colonies rapidly are being outcompeted by the polygyne form, which tends to be even better adapted to disturbed areas. Fire ants are a nuisance to humans and wildlife; control and management of this exotic is important from medical, agricultural, economic, and environmental standpoints (Vinson and Teer 1989, Vinson 1990, MacKay et al. 1992).

Research has suggested that fire ant invasion has resulted in a dramatic decrease in abundance and diversity of native invertebrate communities (Porter and Savignano 1990, Vinson 1991, Stoker 1992) and in the alteration of habitat use by certain vertebrate species (Smith et al. 1990, Stoker 1992, Killion 1992, Ferris 1994, Holtcamp and Grant unpublished manuscript). Fire ants may compete with native species for

food, space, and may provide a predation pressure to which native species have not yet adapted. Thus, examining the impact of fire ants on native species is both an ecologically relevant and important endeavor.

Deer mice are a common cricetine rodent species in North America, with a range that spans from northern Mexico to Canada (Grzimek 1990). Deer mice and fire ants coexist over large portions of the deer mouse's range. The mice are crepuscular to nocturnal (Schmidly 1983). Fire ant activity is maximal when soil temperatures are between 22° to 36° C, although they will forage between soil temperatures of 15° to 43° C (Porter and Tschinkel 1987). Hence, deer mice are most likely to be affected by fire ants during those times of year when nighttime temperature lies within the fire ant's active temperature range, primarily spring through fall.

In deer mice, food intake above the level needed for body maintenance has been shown to affect fighting, escape, and reproduction. Dewsbury (1981) found that heavier males are more likely to win fights, and obtain more copulations than smaller males. Jameson (1953) found that larger females typically carry a higher number of embryos. Thus, it appears that the fitness of deer mice is correlated positively with energy intake. In addition, work by Clarke (1983), Anderson (1987), and Travers et al. (1988) shows that deer mice may alter foraging patterns in response to perceived predation risk. Thus it is likely that deer mice make active decisions to trade off energy intake for survival.

APPENDIX B

PERMISSION LETTER

MEMORANDUM

Mar. 15, 1995

TO: Brian Keller - Permissions Editor - ESA

FROM: Wendee Holtcamp
Dept. Wildlife & Fisheries Sciences
Texas A&M University
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(409) 764-7518 - phone
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SUBJECT: Permission request to use Ecology figure in thesis

Dear Dr. Keller:

I am requesting permission to modify a figure from Valone and Brown's Ecology article, entitled, "Measuring Patch Assessment Abilities of Desert Granivores" for my Master's thesis. This article appeared in the Dec. 1989 issue of Ecology, and the volume and page numbers are 70:1800-1810. I have enclosed a copy of the modified figure. As the deadline for the final draft of my thesis is March 30, I would appreciate if you could fax me the permission, if granted, as per our earlier phone conversation. I appreciate your help in this matter. If there are any further questions, feel free to contact me at the above email address or phone number.

Sincerely,

Wendee Holtcamp

PERMISSION GRANTED TO USE
THE MATERIAL CITED ABOVE

B. D. Keller 16 Mar. 95

BRIAN D KELLER
PUBLISHER
THE ECOLOGICAL SOCIETY
OF AMERICA

---END---

APPENDIX C

FLUON EXPERIMENT RESULTS

TABLE A1. Results of blocked one-factor ANOVAs comparing deer mice use of patches with and without fluon®. In all analyses, the independent variable was fluon, individual mouse was the blocking factor, and sample size was 10. The ANOVAs were conducted on the raw data collected from the trials, from which all further calculations were made.

	Model		Fluon	
Dependent variable	F	p-value	F	p-value
Number of patch visits	2.47	.0943	2.33	.1612
Total foraging time	0.68	.7204	0.33	.5812
Seeds harvested	1.24	.3776	1.33	.2780

VITA

Wendee Nicole Holtcamp was born July 13, 1970 to Diane A. Leonard and Thomas R. Finlay in Mission Hills, California. During her undergraduate career, she worked at LGL Ecological Research Associates as a lab technician from August 1991 through March 1992, and was employed as a research analyst at EG&G Environmental Sciences Department in Nevada in the summer of 1992. She graduated Magna Cum Laude with a Bachelor of Science in Wildlife and Fisheries Sciences at Texas A&M University in May 1993. During the summer of 1993, she was employed as a research technician for Dr. Ken Risenhoover. She began graduate studies at Texas A&M University in the Department of Wildlife and Fisheries Sciences in September 1993, and was awarded a Regents Graduate Fellowship for 1993-1994. At the time of this writing she is employed at Texas A&M University in the Department of Wildlife and Fisheries Sciences as a teaching assistant for Animal Ecology lab. Her permanent mailing address is c/o Diane Leonard, 4003 Black Oak Drive, Carrollton, Texas 75007.